

REVISION OF AN EARLY CRETACEOUS MACROFLORA FROM THE MARYBOROUGH FORMATION, MARYBOROUGH BASIN, QUEENSLAND, AUSTRALIA

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McLoughlin, S. Tosolini, A.P. & Drinnan, A.N. 2000 06 30: Revision of an Early Cretaceous macroflora from the Maryborough Formation, Maryborough Basin, Queensland, Australia. *Memoirs of the Queensland Museum* 45(2): 483-503. Brisbane. ISSN 0079-8835.

An Early Cretaceous (Aptian or earliest Albian) impression flora is described from the upper part of the Maryborough Formation in the Maryborough Basin, southern Queensland. The flora is preserved in marine sediments hosting an abundant invertebrate fauna dominated by bivalve molluscs. The flora incorporates single species attributable to the Polypodiophyta, Pentoxylales and Bennettitales. Two cuneate leaves have affinities either with the Ginkgoales or seed-ferns. Four species of conifer foliage are represented together with araucariacean ovulate cones. Fossils considered by previous workers to be plant roots are reinterpreted as invertebrate burrows, and forms attributed to equisetalean nodal diaphragms may alternatively represent gastropod opercula. An Aptian or earliest Albian age based on past studies of the fossil fauna is supported by the presence of the stratigraphic index fossil *Phyllopteroides serrata* Cantrill & Webb. □ Aptian. *Phyllopteroides*, *Araucariaceae*, *Pentoxylales*, *Bennettitales*, *Cretaceous palaeoenvironments*.

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In 1918, A.B. Walkom described a small assemblage of plant fossils from the Maryborough Formation, Maryborough Basin, SE Queensland. Most of the plant fossils had been collected by Mr Daniel Jemmett and his son during quarrying operations at the Corporation Quarry, Maryborough (Dunstan, in Walkom, 1918). The plant remains were illustrated with a series of simple line-drawings, which in some cases did not express the full suite of morphological characters available in the fossils. Since that date, improved understanding of the systematics, phylogenetic affinities, and stratigraphic ranges of some plant groups has necessitated revision of some of Walkom's identifications. Several plant fossils from the Maryborough Formation, including counterparts of some of Walkom's studied specimens, were subsequently sent to the Natural History Museum, London, by B. Dunstan, then Queensland Chief Government Geologist. This paper presents revised systematic descriptions of the Maryborough Formation macroflora. The study is part of a broader project to describe and revise a series of fossil floras from eastern Australia in order to better resolve the stratigraphic and palaeobiogeographic ranges of Mesozoic plant taxa.

GEOLOGICAL SETTING

The Maryborough Basin (Fig. 1) covers an area of around 24,600 km² and incorporates a terrestrial, paralic and marine succession at least

4000m thick. Subsidence in the Maryborough Basin initiated during latest Triassic times was roughly contemporaneous with development of the contiguous Nambour, Clarence-Moreton, Surat, Eromanga, Carpentaria, and Laura basins elsewhere in Queensland. Initial deposits in the basin are represented by the uppermost Triassic to Lower Jurassic, Myrtle Creek Sandstone (Fig. 2) deposited predominantly in high-energy fluvial settings (Cranfield, 1993). Subsequently, the Tiaro Coal Measures (Lower to ?Middle Jurassic) were deposited in a range of fluvial settings dominated by high-sinuosity rivers and incorporating extensive floodbasin mire deposits. The Tiaro Coal Measures also incorporate a distinctive 30m thick interval containing prominent beds of pisolitic and oolitic ironstone that are useful marker horizons for correlation with sequences in neighbouring basins (Cranfield, 1993). The Grahams Creek Formation (?Upper Jurassic to ?Neocomian) unconformably overlies the Tiaro Coal Measures, but the hiatus in sedimentation is not well resolved due to poor palynological age constraints on the upper Tiaro Coal Measures and entire Grahams Creek Formation (Cranfield, 1993). The Grahams Creek Formation is dominated by intercalated intermediate to felsic volcanics and volcanigenic sediments. The unit was deposited in continental settings and some sediments have

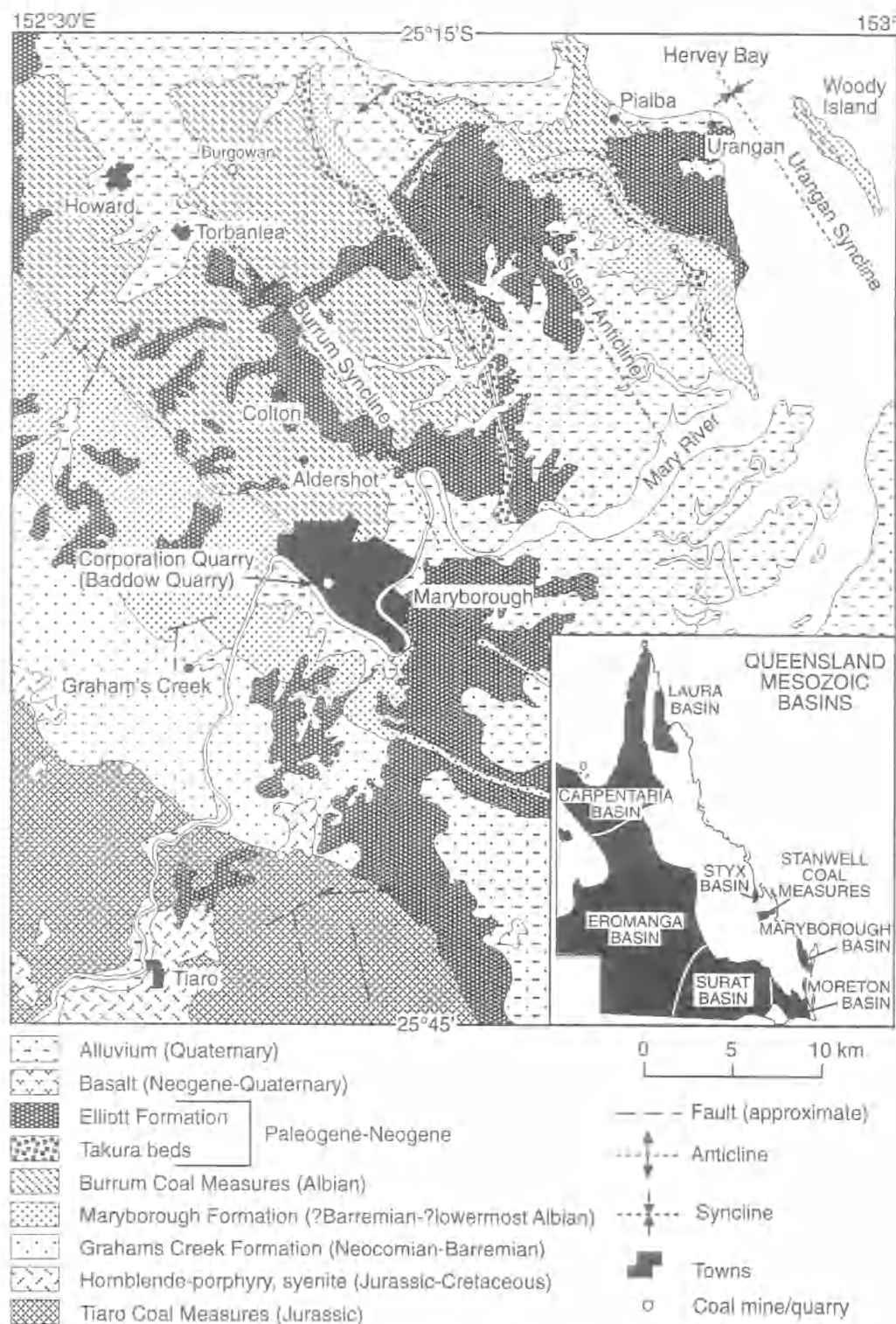


FIG. 1. Geological map of the Maryborough district showing the location of Corporation Quarry, the main site yielding plant fossils.

STAGE		MARYBOROUGH	SURAT	EROMANGA	OTWAY/ GIPPSLAND
CRETACEOUS	TURONIAN				Flaxman Fm Waarre Fm
	CENOMANIAN			Winton Fm	
	ALBIAN			Mackunda Fm	
			Griman Ck Fm	Allaru Mst	
	APTIAN	Burrum Coal Measures	Surat Siltst	Toolebuc Fm	
			Wallumbilla Formation	Wallumbilla Formation	Eumeralla Formation
		Maryborough Formation			"Wonthaggi Formation"
	BARREMIAN		Bungil Formation	Cadna-owie Formation	
	NEOCOMIAN				Crayfish Subgroup
	Haut.	?			Rintoul Ck Formation
JURASSIC	Val.		Mooga Sandstone	Hooray Sst	Tyers Cong.
	Berr.	Grahams Creek Formation	Orallo Fm Gubb. Sst		
			West. Fm	Westbourne Fm	Casterton Fm
	LATE			Adori Sst	
	Tith.	?	Pilliga Sst		
	Kimm.			Injune Ck Grp	
	Oxf.		Walloon C.M.	Birkhead Formation	
	MIDDLE		Mulgildie Coal Measures		
	Call.		Purlawaugh Fm		
	Bath.				
	Baj.	Tiaro Coal Measures	Hutton Sandstone	Hutton Sandstone	
	Aal.				
	EARLY		Evergreen Boxvale Sst	Boxvale Sst	
	Toar.		Formation		
	Plien.				
	Sin.	Myrtle Creek Sandstone	Precipice Sst	Precipice Sst	
	Hett.				

FIG. 2. Stratigraphic chart showing correlation of the Maryborough Basin succession with sequences in the Surat, Eromanga, and southern Victorian basins. Leaf symbol indicates plant-bearing unit.

been interpreted as the deposits of alluvial fans (Cranfield, 1993).

The disconformably overlying Maryborough Formation (?Neocomian to ?lowermost Albian) was deposited in a range of sedimentary environments. The formation ranges in thickness from 600 to 2500m (Day et al., 1983). The basal conglomeratic beds were probably deposited in continental settings (Draper, 1971) but a subsequent (late Neocomian) marine transgression saw the remainder of the formation deposited in a mosaic of paralic to shallow marine settings. Sandstones within the unit have been identified as potential hydrocarbon reservoir targets (Siller, 1961; Ellis, 1966). The assemblage of plant remains studied here is derived from the upper part of the formation where invertebrate macrofossils are also abundant. The conformably overlying Burrum Coal Measures (?lower to middle Albian) were deposited within fluvial settings hosting extensive peat-forming mires in floodbasin environments. Sedimentation ceased after deposition of the Burrum Coal Measures (Fig. 2) and the basin was subjected to faulting and moderate folding before deposition of fluvio-lacustrine Elliot and Takura formations in the mid-Cenozoic.

Gentle post-Albian deformation was probably associated with the breakup of Australia and Tasmantis (comprising New Zealand, the Lord Howe Rise, and associated submarine plateaux) and asymmetrical opening of the Tasman Sea (Coleman, 1980; Bryan et al., 1997). As a result of this deformation, the Maryborough Formation is now exposed along the flanks of a series of NW-SE trending anticlines/synclines (Fig. 1).

MATERIAL AND METHODS

Material from the Maryborough Formation held in the collections of both the Geological Survey of Queensland, Brisbane (prefixed QSQF), and the Natural History Museum, London (prefixed NHMV) was investigated. All studied specimens are derived from Corporation Quarry, also known as Baddow Quarry (Fleming, 1966b) in the western part of Maryborough city near the junction of the main Aldershot railway with the Brisbane-Maryborough railway (Fig. 1). Specimens cited by Walkom (1918) as being from 'Argyle Creek, three miles northwest of Aldershot' are probably derived from the overlying Burrum Coal Measures. All of the plant fossils are from the upper part of the Maryborough Formation and are preserved as impressions (lacking cuticular details) in pale

grey, commonly silicified, siltstone. All specimens were illustrated under strong unilateral, low-angle light using Kodak Techpan film. Line-drawings were composed from photo-enlargements.

SYSTEMATIC PALAEOBOTANY

POLYPODIOPHYTA OSMUNDALES OSMUNDACEAE

Phyllopteroides (Medwell) emend. Cantrill & Webb 1987

TYPE SPECIES. *Phyllopteroides dentata* (Medwell) Cantrill & Webb 1987; upper Eumeralla Formation (Albian); Killara Bluff, Otway Basin, Victoria.

Phyllopteroides serrata Cantrill & Webb 1987 (Fig. 3A-C)

Sphenopteris sp. Walkom, 1918: p. 6; pl. 1, figs 4,5.

MATERIAL. HOLOTYPE: NMVP167486; Koonwarra fish beds, upper Strzelecki Group (Aptian); Koonwarra, Gippsland Basin, Victoria (Cantrill & Webb, 1987). OTHER MATERIAL: GSQF959a,b, NHMV24605.

DIAGNOSIS. See Cantrill & Webb (1987, p. 66).

DESCRIPTION. This species is represented by isolated lanceolate to ?oblanceolate pinnules 38-53mm long and 10-12mm wide. The base of each pinnule is not preserved; apices are acute and finely toothed. Pinnule margins are undulate or weakly crenate with typically four denticles developed on each lobe (Fig. 3B). Denticles are less than 0.5mm long and broad and each one corresponds to a vein terminus. The midrib is robust (1mm wide) in the proximal portion of the pinnule but tapers and becomes indistinct in the distal part (Fig. 3A). Lateral veins are alternate, depart acutely from the midrib, arch slightly across the lamina and intersect the margin at 25-40°. Vein density is 4-6 per 5mm along the margin. One specimen (GSQF959a, Fig. 3C) is obovate, has more densely spaced venation and the margins are not clearly denticulate.

REMARKS. Specimen GSQF959a is atypical and may represent a separate taxon but it is an incompletely preserved pinnule. *Phyllopteroides lanceolata* (Walkom) Medwell, 1954 from the Albian Burrum and Styx coal measures in the Maryborough and Styx basins of Queensland is morphologically closest to *P. serrata* but is distinguished by its greater vein density (9-16 per 5mm) and more obtuse secondary veins (marginal angles of 50-70°). *Phyllopteroides dentata* Medwell, 1954, known only from Albian strata

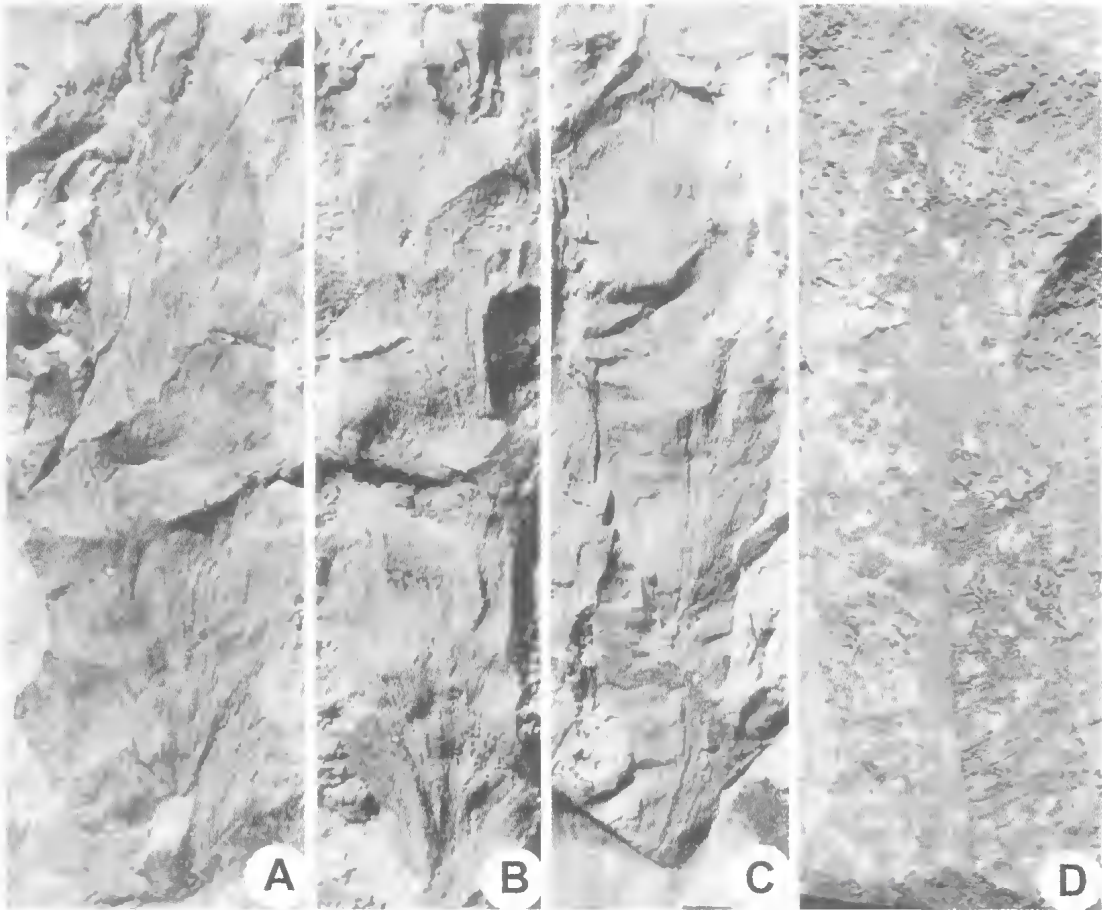


FIG. 3. A-C, *Phyllopteroides serrata* Cantrill & Webb 1987. A, Pinnule with undulate and denticulate margins, NHMV24605 $\times 3$; B, pinnule with denticulate margins, GSQF959b $\times 3$; C, atypical obovate pinnule, GSQF959a $\times 2$. D, *Taeniopteris daintreei* McCoy 1874, apex of leaf, GSQF836 $\times 5$.

of the Otway Basin is a much larger leaf with deeply dentate margins. *Phyllopteroides laevis* Cantrill & Webb, 1987 and *P. westralensis* McLoughlin, 1996 from the Victorian, Queensland and Western Australian Neocomian-Barremian strata are distinguished from *P. serrata* by their finely denticulate or entire margins. In most cases, *P. laevis* also differs in shape having elliptical pinnules. *Phyllopteroides macclymontae* from the Cenomanian Winton Formation, Eromanga Basin, generally has more obtuse venation and a more finely denticulate margin than *P. serrata*.

DISTRIBUTION. Aptian to basal Albian strata of the Gippsland and Otway basins, Victoria (Cantrill & Webb, 1987); and Maryborough Formation (Aptian or lowermost Albian) of the Maryborough Basin, Queensland.

GYMNOSPERMS

?BENNETTITOPSIDA PENTOXYLEALES

Taeniopteris Brongniart 1832

TYPE SPECIES. *Taeniopteris vittata* Brongniart 1832; Jurassic; Whitby, England.

Taeniopteris daintreei McCoy 1874 (Figs 3D, 4A,C)

Taeniopteris elongata Walkom, 1918: p. 6; pl.1, figs 1-3.
Taeniopteris Tenison-Woodsii (Etheridge Jr) Walkom, 1918: p. 8.
Taeniopteris sp. Walkom, 1918: p. 8.

LECTOTYPE. NMVP12270; upper Strzelecki Group (Aptian); Cape Paterson, Gippsland Basin, Victoria, Australia (selected by Drinnan & Chambers, 1985).

MATERIAL. GSQF836, GSQF843, GSQF845, GSQF846, GSQF958, GSQF961, GSQF962; NHMV24613.

DIAGNOSIS. See McCoy (1875: 15), Seward (1904: 168) and Drinnan & Chambers (1985: 90) for diagnostic characters.

DESCRIPTION. No complete leaves have been preserved. Leaves are elongate spatulate, with entire to slightly undulate margins tapering gently to form a narrow, cuneate, acute base (Fig. 4A). Leaves reach >120mm long and 13-21mm wide. One leaf tip bears a pointed acute apex (Fig. 3D). The prominent midrib is stout, usually 1.5-2mm wide, and narrows towards the apex. Secondary veins are subparallel at 70°-90° to the midrib becoming more acute (50°-60°) towards the apex (Figs 3D, 4C). They dichotomize at or very near the midrib producing a tuning fork shape; few divide further away. Vein density is approximately 18 per 5mm at the margin.

REMARKS. Walkom assigned the *Taeniopteris* specimens from the Maryborough Formation (Walkom, 1918) and Burrum Coal Measures (Walkom, 1919) to several species, however, there is insufficient morphological evidence to establish that these leaves represent distinct taxa. Australian Jurassic-Cretaceous *Taeniopteris* leaves show few consistent morphological distinctions between established species. Taxa have been differentiated on the basis of secondary venation angles, margin form and average size (McLoughlin & Drinnan, 1995). However, Drinnan & Chambers (1985) showed that *Taeniopteris daintreei* leaves may incorporate a considerable range of forms at a single locality. Most Jurassic to Cenomanian specimens from all parts of Australia (e.g. forms illustrated by Seward, 1904; Walkom, 1921; White, 1981; Glaessner & Rao, 1955; Gould, 1980; Douglas, 1969, 1973; Drinnan & Chambers, 1985, 1986; McLoughlin et al., 1995; McLoughlin, 1996) are now assigned to, or closely compared with, *Taeniopteris daintreei* in its broader sense (Drinnan & Chambers, 1985). *Taeniopteris howardensis* described by Walkom (1919) from the Burrum Coal Measures is a small obovate leaf that probably represents an end member of the morphological spectrum encompassed by *T. daintreei*. Australian species are also morphologically comparable to the Early Cretaceous *T. spatulata* from India (Bose & Banerji, 1981) and *T. stipulata* from New Zealand (McQueen, 1956). Clear demarcation between these species on gross morphological features is not possible but cuticular differences may be present (Douglas, 1969; Drinnan & Chambers, 1985). Additionally, Drinnan & Chambers (1985) noted

that *Taeniopteris* leaves were associated with different microsporangia (*Sahnia*) and fruits (*Carnoconites*) in India, Australia and New Zealand and on this basis we consider it preferable to retain the Australian leaves in *T. daintreei*.

DISTRIBUTION. Widely distributed in Australian basins in Middle Jurassic (Walkom, 1921) to Aptian (Douglas, 1969) strata. *Taeniopteris* leaves from Albian and Cenomanian strata of the Maryborough and Eromanga Basins (Walkom, 1919; McLoughlin et al., 1995) are closely comparable to *T. daintreei*.

BENNETTITALES

Otozamites Braun in Münster, 1843

TYPE SPECIES. *Otozamites (Zamites) brevifolius* Braun in Münster, 1843. (See Watson & Sincok, 1989 for discussion of typification).

DISCUSSION. Bennettite foliage genera are typically discriminated on the basis of cuticle data and the shape of pinna bases (Watson & Sincok, 1992). *Ptilophyllum* species are defined by having a decurrent, basiscopic, pinnule base whereas *Otozamites* species have an auricle on the acroscopic side of the base. Bose & Kasat (1972) and Bose (1974) reassigned many Indian species of *Otozamites* to *Ptilophyllum*, leaving only five species within *Otozamites*. However, Bose & Kasat (1972) noted that many of the Indian *Ptilophyllum* species have characteristics that are gradational between the two genera, with regard to the definitions used by Watson & Sincok (1992). Harris (1969) and Watson & Sincok (1992) also discussed gradational characteristics between these bennettite genera. *Otozamites* and *Ptilophyllum* may be useful as descriptive form genera but their separation may not have phylogenetic significance.

Otozamites sp. (Fig. 4B)

Ptilophyllum (Williamsonia) pecten (Phillips) Walkom, 1918: p. 10; pl. 1, fig. 7.

MATERIAL. GSQF957.

DESCRIPTION. The single available incomplete frond is pinnate but its gross shape is indeterminate. The frond is 7mm wide and has a length >45mm (total estimated length about 150mm). The rachis is 0.5mm wide. The pinnule bases are not preserved completely so their insertion on the rachis is not clear. The bases appear to expand on the acroscopic side and may form an auricle. On the basiscopic side, the bases appear to contract.

Adjacent pinnules are slightly imbricate, falcate, with pointed, acute and distally inclined apices (Fig. 4B). The pinnules arise at 50°–70° from the rachis and reach 4.5mm long and 1.75mm wide (average = 4 × 1mm). Veins emerge from the centre of pinnule bases and are divergent, dichotomous and lack anastomoses. Around 3–4 veins are evident across the centre of the pinnules.

REMARKS. Based on the slightly expanded acroscopic bases of some pinnules we assign this frond to *Otozamites*. However, the incomplete specimen lacks key frond features and cuticle details to enable assignment to an established species. Walkom (1918) assigned this specimen to *Ptilophyllum pecten* based on comparisons with fronds from the Stanwell Coal Measures, Queensland (Neocomian), and the Yorkshire Jurassic. Both the Stanwell specimens (Walkom, 1917), and the Maryborough Formation frond are transferable to *Otozamites*. The Maryborough form has similarities to bennettite impressions described previously from India as *Otozamites bengalensis* (Oldham & Morris, 1863), *Ptilophyllum cutchense* (Bose & Kasat, 1972) and with the smaller, basal pinnae of *Ptilophyllum acutifolium* fronds (Bose & Kasat, 1972). *Otozamites bengalensis* has been reassigned both to *Ptilophyllum acutifolium* (Bose, 1974) and *Ptilophyllum cutchense* (Bose & Kasat, 1972). It is possible that the morphology of fronds from a single plant may have varied sufficiently to account for the differences between these form species but without cuticular evidence this cannot be verified. Within Australia, the Maryborough Formation specimen most closely resembles leaves from: the Neocomian Algebuckina Sandstone in South Australia (*Otozamites bengalensis* in Glaessner & Rao, 1955); the Neocomian-Barremian Broome Sandstone and Leederville and Bullsbrook Formations, Western Australia (described as *Ptilophyllum cutchense* by McLoughlin, 1996); the Neocomian Stanwell Coal Measures, Queensland (assigned to *P. pecten* by Walkom, 1917); and the Albian Burrum Coal Measures (assigned to *P. pecten* by Walkom, 1919).

DISTRIBUTION. Maryborough Formation, Maryborough Basin, Queensland. Comparable forms are discussed above.

PINALES ARAUCARIACEAE

Araucariacean ovulate cones (Figs 4E, 5B)

Araucarites polycarpa Tenison-Woods. Walkom, 1918: p. 10.
Araucarites sp. Walkom, 1918: pl. 2, fig. 10.

MATERIAL. GSQF842, GSQF853.

DESCRIPTION. Two cones are available; one (GSQF853) is preserved as a slightly off-centred axial impression (Figs 4E, 5B), the other (GSQF842) is an incomplete lateral impression (Fig. 5B). The cones are circular in transverse section and elliptical or oblong in longitudinal section. The cones are 25–28mm in diameter and >55mm long (apex and base absent). The cones are composed of tightly packed, helically arranged scales with transversely elongate apical ends. Scale apices are 4–7mm wide and 2–3mm deep. The apices are truncate to gently rounded, or in some cases may have a short, blunt point, but prominent spines are absent. Although the cone compressed in an apical orientation has undergone slight distortion, an 8:13 phyllotaxy is evident (Fig. 5B).

REMARKS. We refrain from placing these cones in an established taxon or under new nomenclature owing to the dearth of available cone-scale characters. The absence of prominent apical spines on the cone scales favours an affinity with *Agathis* rather than *Araucaria* or *Wollemia* amongst extant Araucariaceae. Walkom (1918) assigned these specimens to two species of *Araucarites* but there are insufficient morphological differences to warrant specific differentiation. Numerous detached araucariacean cone scales have been described from the Australian Mesozoic (e.g., Walkom, 1921; Drinnan & Chambers, 1986; McLoughlin et al., 1995). However, the absence of any detached cone scales in the Maryborough assemblage prevents assessment of whether the seeds were shed independently of the scale (as in modern *Agathis* and *Wollemia*) or whether the scales retained their seeds (as in *Araucaria*) after detachment from the cone. Similar cone fragments with tight, spirally arranged scales occur in the Stanwell Coal Measures near Rockhampton (Walkom, 1917), although the scale apices of the Maryborough species are about twice as broad. Substantially smaller and narrower araucariacean cones were recorded from the Victorian upper Strzelecki Group (Drinnan & Chambers, 1986: fig. 30A,B) but it is

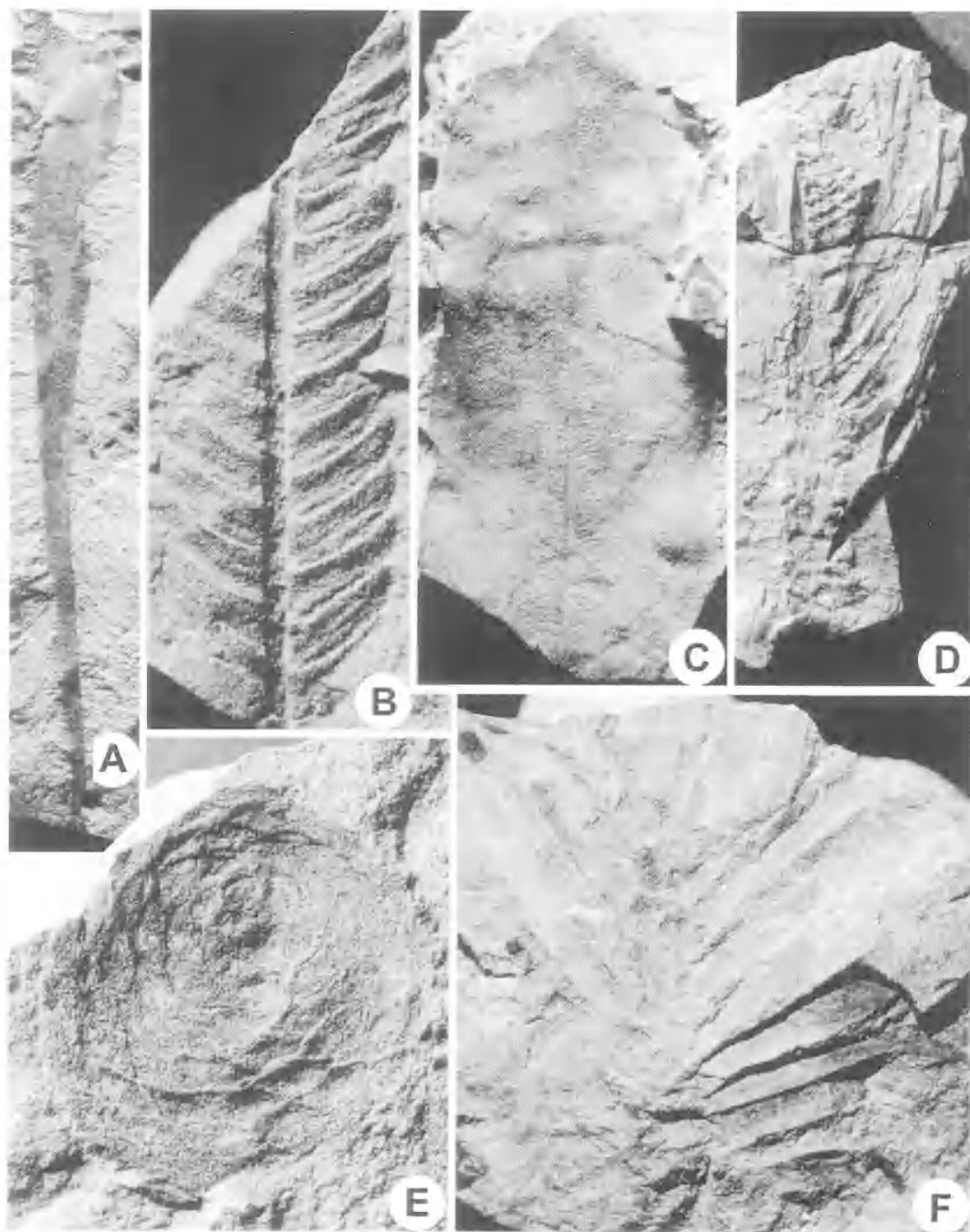


FIG. 4. A, C, *Taeniopteris daintreei* McCoy 1874; A, elongate leaf showing gently tapering base, GSQF845 $\times 1$; C, broad leaf with undulate margins showing venation details, GSQF961 $\times 2$. B, *Otozamites* sp., fragment of pinnate frond, GSQF957 $\times 5$. D, E, *Podozamites mesozoica* Walkom comb. nov.; D, axis with rhythmic growth increments, GSQF954 $\times 1$; E, terminal portion of axis with helically arranged leaves, NHMV24611 $\times 2$. F, near-axial impression of an araucariacean ovulate cone, GSQF853 $\times 2$.

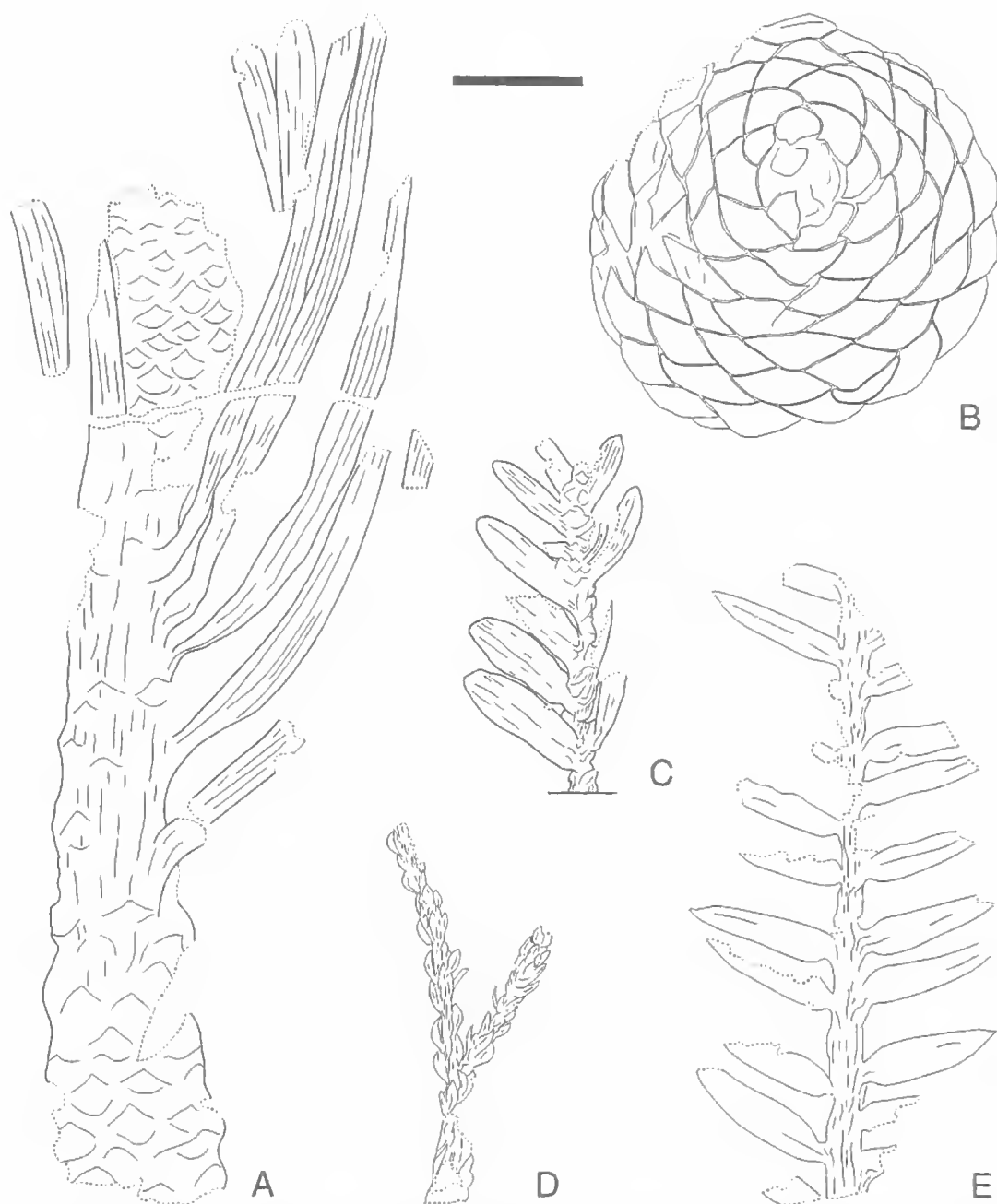


FIG. 5. Line-drawings of conifer remains from the Maryborough Formation. A, *Podozamites mesozoica* Walkom comb. nov., GSQF954; B, Araucariacean ovulate cone, GSQF853; C, *Pagiophyllum jemmetti* Walkom 1918, GSQF1133; D, *Pagiophyllum* sp., NHMV24614; E, *Elatocladus baddowensis* sp. nov., GSQF853. Scale bar = 10mm.

unclear whether the Victorian specimens represent complete cones, cone axes, or even whether these cones were ovulate or microsporangiate.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Maryborough Basin; possibly Stanwell Coal Measures (Neocomian), Yarrol Block, Queensland.

INCERTAE FAMILIAE

Podozamites (Brongniart) Braun 1843

TYPE SPECIES. *Podozamites distans* (Presl) Braun, in Münster 1843; Lower Liassic, Bayreuth, Bavaria.

Podozamites mesozoica Walkom comb. nov.
(Figs 4D,F, 5A, 6A,E)

Araucurites mesozoica Walkom, 1918: p. 11; pl. 2, figs 1-3.

MATERIAL. LECTOTYPE: GSQF954 (Figs 4D, 5A, 6E); Baddow Quarry, Maryborough Formation (Aptian or earliest Albian), Maryborough, Queensland (here designated). OTHER MATERIAL. NHMV24610, NHMV24611.

DIAGNOSIS. Stout axes with rhombic leaf scars showing rhythmic growth increments or bearing linear leaves with around 4 parallel veins. Leaves slightly tapered but connected to axis by a broad base, apices rounded.

DESCRIPTION. Axes reaching >66mm long and up to 9mm thick bearing spirally arranged, linear, multiveined leaves (Figs 4D,F, 5A, 6E). Leaf scars on the axis are broadly rhombic, mostly 3mm wide, and 1.5-3mm high. The distal adaxial margin of each leaf scar is typically more deeply impressed into the sediment matrix than the proximal (abaxial) margin. Variable leaf scar spacing along the axis represents rhythmic growth increments (Figs 4D, 5A, 6A). Scar spacing varies from 2-3mm (separated by featureless areas of the axis) to closely abutting. The leaves are linear, 20->40mm long, 2.5-3mm wide. The entire margins gently taper towards the base but the leaves retain a broad basal attachment; leaf apices are blunt to rounded. The leaves are arrayed at 20-70° from the axis and may be straight, or gently inflexed or reflexed. At least four parallel veins are present in each leaf; dichotomies and anastomoses are not evident.

REMARKS. The lectotype selected here is the only specimen of this species figured by Walkom (1918). The cone-like feature reported by Walkom (1918) at the distal end of this specimen (Fig. 4D, 5A) is here interpreted to be a region of closely abutting rhomboid leaf scars. The species is transferred to *Podozamites* (Presl) Braun, a genus used for coniferous remains of uncertain familial affinity having strap-shaped leaves with several longitudinal veins. *Araucurites* by contrast is typically applied to isolated cone-scales of araucariacean affinity (Taylor & Taylor, 1993). Some *Podozamites* species may be allied to the Araucariaceae but a lack of cuticle characters or

attached fruits for *P. mesozoica* prevents definite assignment to an established conifer family. Several *Podozamites* species were described from the overlying Burrum Coal Measures (Albian) in the Maryborough Basin by Walkom (1919) but these all have substantially smaller leaf length:width ratios than *P. mesozoica*. Cantrill (1991) described three *Podozamites* species with preserved cuticle from the Albian part of the Otway Group of Victoria. Of these taxa *P. taenioides* and *P. notabilis* can be distinguished by their distinctly decurrent leaf bases. *Podozamites pinnatus* is similar to *P. mesozoica* in its more abbreviated, rhombic leaf base and the presence of around four prominent veins/striations in the lamina but the leaves of the former are typically twice as wide. Some forms of the conifer complex assigned to *Araucaria* sp. cf. *A. mesozoica* from the Winton Formation (Cenomanian) of Queensland by McLoughlin et al. (1995) are similar to the Maryborough species. However, the Winton Formation forms mostly have broader leaves with more numerous veins. Nevertheless, the Winton forms do show rhythmic leaf development on the axes (Dettmann et al., 1992) suggesting a similar seasonal growth habit. *Podozamites mesozoica* is also comparable in terms of gross morphology to the foliage of other fossil genera such as *Lindleycladus* Harris (1979) but these are generally differentiated on the basis of cuticular features that are unavailable in the Maryborough specimens.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Queensland.

INCERTAE FAMILIAE

Pagiophyllum Heer 1881 emend. Harris 1979

TYPE SPECIES. *Pagiophyllum circinicum* (Saporta) Heer 1881; Upper Jurassic, Sierra de San Luiz, Portugal.

Pagiophyllum jemmetti Walkom 1918
(Figs 5C, 6C,D, 7A, C)

Pagiophyllum Jemmetti Walkom, 1918: p. 13; pl. 2, figs 7,8.

MATERIAL. LECTOTYPE: Here selected as GSQF1133 (Figs 5C, 6D); illustrated by Walkom (1918; pl. 2, fig. 7). GSQF851, GSQF952, GSQF953, GSQF956, NHMV24608.

DIAGNOSIS. Straight ultimate shoots bearing densely packed, helically arranged, oblong, ovate, to awl-shaped leaves lacking cuticle, inserted at 45-90° to the axis. Leaf length:width ratio 2:1-4:1.

DESCRIPTION. Axes reaching >76mm long and 6mm wide, bearing spirally arranged leaves. The

leaves are oblong, ovate or awl-shaped, closely spaced but spreading, and inserted at 45-90° to the axis (Figs 5C, 6D, 7A,C). The leaves are thick at the base but otherwise dorsiventrally flattened, straight or slightly inflexed (Fig. 6C,D). The leaves are 5-13mm long, 1.5-5.5mm wide, with rounded or obtusely pointed apices and broadly attached or slightly decurrent bases. Where the leaves are broken or detached a 2.5mm wide, 1-2 mm high rhombic scar is retained on the axis. The leaf margins are entire. The leaves generally possess >2 parallel longitudinal striations per leaf but the venation is generally indistinct.

REMARKS. A specific diagnosis is provided here as Walkom (1918) gave only a general description of this taxon. Axes with similar crowded, short, lanceolate leaves from the Broome Sandstone (Neocomian) assigned to *Araucaria* sp. C by McLoughlin (1996) are distinguished by their acutely pointed leaf apices. A number of Laurasian *Pagiophyllum* species have grossly similar morphology to *P. jemmetti* (see for example: Harris, 1979) but these are mostly differentiated on cuticular characters unavailable in the Maryborough specimens. *Pagiophyllum jemmetti* can, nevertheless, be distinguished from most species by its densely crowded, spreading foliage, relatively low leaf length:width ratio and blunt leaf apices. *Pagiophyllum*- or *Geinitzia*-type remains from the Early Cretaceous of southern Australia are generally typified by smaller, narrower, acutely inserted leaves (Cantrill & Douglas, 1988).

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Maryborough Basin, Queensland.

***Pagiophyllum* sp. A**
(Figs 5D, 8C)

MATERIAL. NHMV24614.

DESCRIPTION. This branched twig bears spirally arranged, awl-shaped leaves (Figs 5D, 8C). The axes are >26mm long (apex not preserved), <1mm wide and branch at 15-20°. The leaves are 2mm long, 0.75mm wide and 0.5mm thick. They are univeined and most are closely appressed to the axis, slightly overlapping the bases of leaves in the succeeding spiral. In a few cases the leaves are slightly divergent from the axis. Deep imprints in the sediment left by some leaves suggest that they were trifacial (i.e., they possessed a prominent abaxial keel). The leaves are broadly based and

perhaps slightly decurrent. The apices are blunt and incurved, and the margins are entire.

REMARKS. Walkom (1918) either overlooked this species or the specimen was not available in his studied collections. The only available specimen is currently held in the collections of the Natural History Museum, London. The generic boundaries between *Pagiophyllum*, *Brachyphyllum* and *Geinitzia* are arbitrary and differentiation of these form genera has little phylogenetic meaning at present. *Brachyphyllum* has leaves that are shorter than broad, *Geinitzia* has leaves that are as thick as they are broad, and *Pagiophyllum* typically has leaves that are longer than broad and broader than thick. The Maryborough specimen is therefore assigned to *Pagiophyllum* but the poor preservation of the single available specimen prohibits confident assignment to an established species or warrants erection of a new species. It is similar in leaf size, shape and arrangement to some specimens assigned to cf. *Austrosequoia wintonensis* Peters & Christophel 1978 from the Winton Formation, Queensland, and to *Araucaria* sp. A of McLoughlin (1996) described from the Broome Sandstone (Neocomian), Western Australia.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian). Several other fossils from northern Australia of Neocomian-Cenomanian age are closely comparable.

INCERTAE FAMILIAE

***Elatocladus* Halle emend. Harris 1979**

TYPE SPECIES. *Elatocladus heterophylla* Halle 1913; Jurassic, Hope Bay, Graham Land, Antarctica.

***Elatocladus baddowensis* sp. nov.**
(Figs 5E, 7B,D, 8A,B)

?*Pterophyllum* sp. Walkom, 1918: pl. 1, fig. 6.

?*Taxites* sp. Walkom, 1918: p. 13; pl. 1, fig. 9.

MATERIAL. HOLOTYPE: GSQF853 (Fig. 5E, 7B), counterpart = NHMV24609 (Fig. 7D); Baddow Quarry (Corporation Quarry), Maryborough Formation (Aptian or earliest Albian), Maryborough, Queensland. OTHER MATERIAL: GSQF838, GSQF7267, NMHV24606, NHMV24609.

DIAGNOSIS. Slender axes with spirally inserted but basally twisted leaves forming a distichous, opposite to sub-opposite arrangement. Leaf bases slightly contracted and decurrent for 1-2mm along axis. Leaves oblong to lanceolate

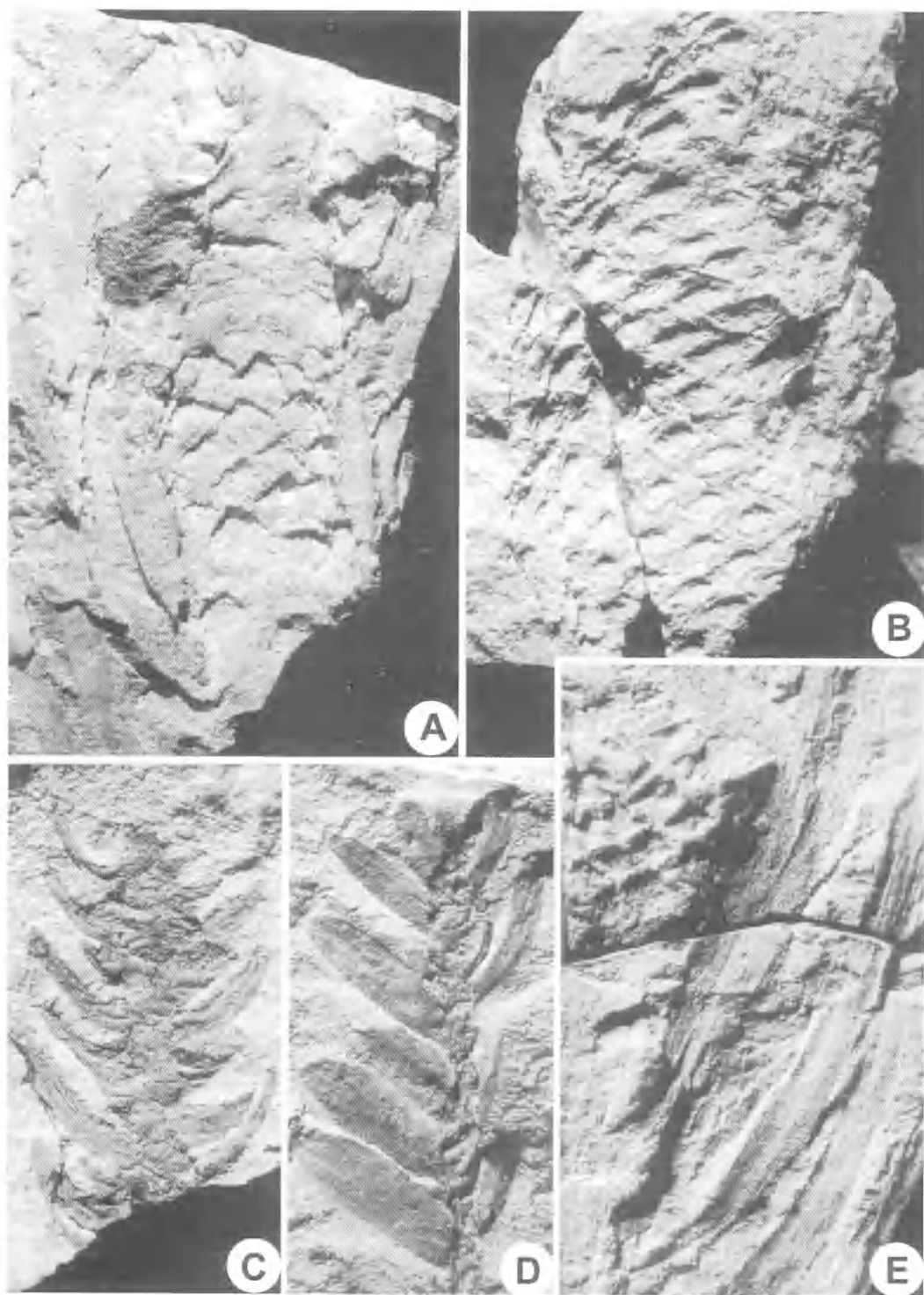


FIG. 6. A, E, *Podozamites mesozoica* Walkom comb. nov.; A, stout axis with rhombic leaf scars and linear leaves, NHMV24610 $\times 3$; E, details of venation and leaf attachments, GSQF954 $\times 3$. B, lateral impression of an araucariacean ovulate cone, GSQF842 $\times 2$. C, D, *Pagiophyllum jemmetti* Walkom 1918; C, lateral imprint showing awl-shaped leaves, GSQF952 $\times 3$; D, terminal portion of branch with oblong leaves, GSQF1133 $\times 3$.

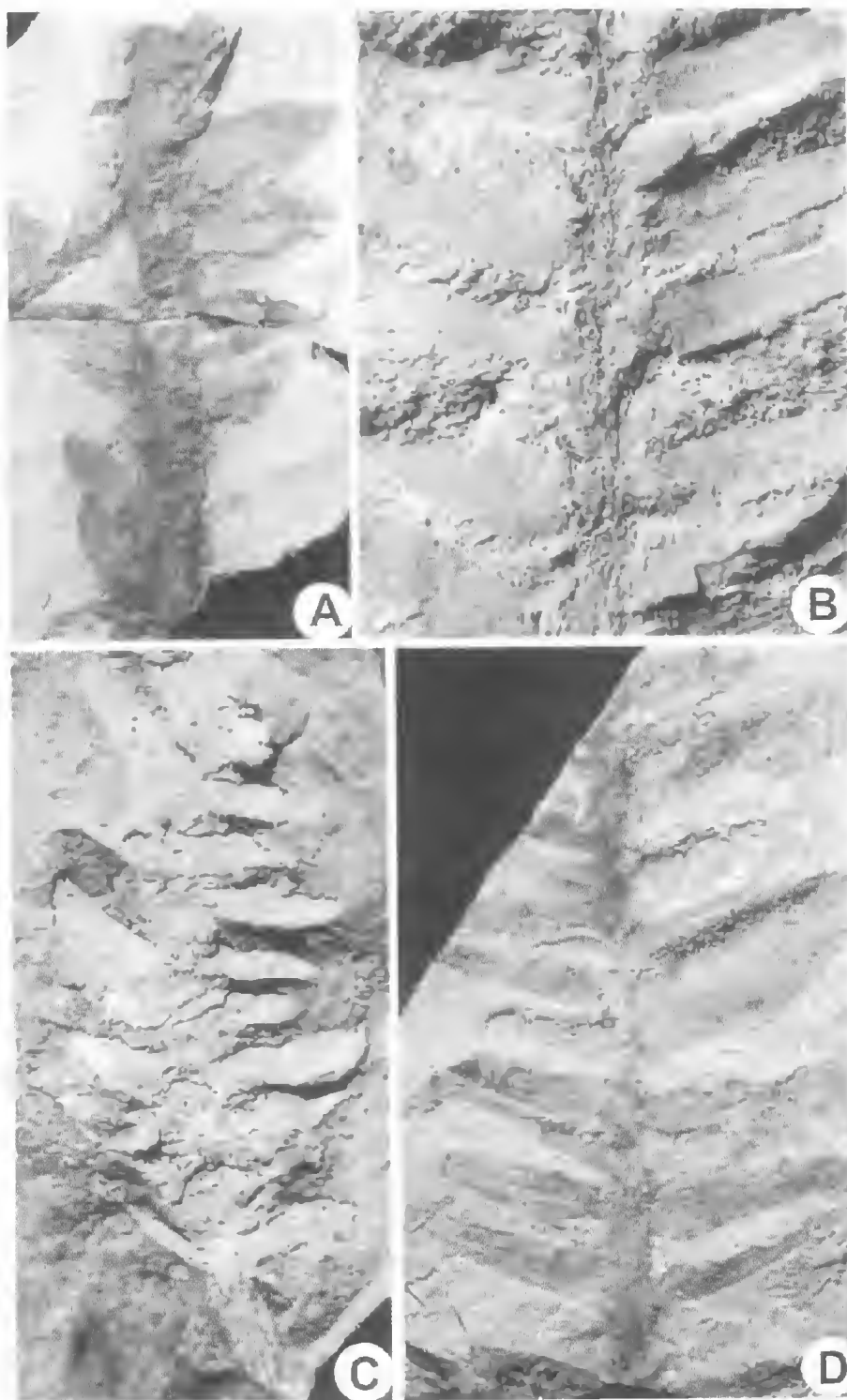


FIG. 7. A, C, *Pagiophyllum jemmetti* Walkom 1918; A, stout axis with ovate leaves, NHMV24608 $\times 2$; C, axis with helically arranged leaves, GSQF956 $\times 3$. B, D, *Elatocladus baddowensis* sp. nov.; B, details of leaf insertion on the axis, GSQF853 $\times 4$; D, twig bearing univeined, distichous leaves, NHMV24609 $\times 3$.

with a length:width ratio of 4.5:1 to 5.5:1. Venation ill-defined and cuticle unknown.

DESCRIPTION. Slender (1.5-3mm wide) axes reaching >41 mm long, bearing spirally inserted but basally twisted leaves in a distichous arrangement (Figs 7B,D, 8A,B). The leaves are opposite to sub-opposite, and leaf pairs are typically 1.5-2mm apart. Leaves are 6-17mm long and 1.5-2.5mm wide. They are typically straight or slightly inflexed and arranged at 45-80° to the axis. Leaves are dorsiventrally flattened and slightly contracted towards the base (Fig. 7B). The leaves are oblong to lanceolate with rounded apices and entire margins. The base may be decurrent for 1-2mm along the axis. The venation is generally indistinct. A single median vein is evident on a few leaves and several parallel striations are evident on others.

REMARKS. *Elatocladus* has been used for conifer remains of widely varying morphology since its erection by Halle (1913). Some, like specimens assigned to *Elatocladus planus* (Feistmantel) Seward from the Jurassic Talbragar fish beds of New South Wales (Walkom, 1921), have atypical features such as transverse striae on the lamina and probably warrant generic segregation. Some species have a spiral arrangement of leaves whereas others show a distinctly distichous arrangement. Harris (1979) provided the history of generic emendations for *Elatocladus*. It is employed here in its broadest sense (Harris, 1979) to include 'fossil conifer shoots bearing elongated, dorsiventrally flattened leaves with a single vein. Leaves divergent from the stem'. Basal twisting of the spirally inserted leaves to a distichous arrangement is common amongst *Elatocladus* species but the majority of forms assigned to this genus have a more contracted, commonly petiolate, leaf base. Most *Elatocladus* species, and forms assigned to the morphologically similar genera *Rissikia* Townrow 1967 and *Mataia* Townrow 1967, have a more prominent midrib in the leaves than *E. baddowensis*. The leaves of this species may have developed ill-defined longitudinal creases during desiccation giving the false impression of multiple veins in the lamina. Longitudinal creasing and basal twisting of the leaves is similar to that illustrated by Florin (1931) for extant *Podocarpus rospigliosii*. A podocarpacean alliance is possible for *E. baddowensis* given the podocarpacean affinities of morphologically similar foliage from the Australian Mesozoic (Townrow, 1967, 1969). However, if the sparse

longitudinal creases represent multiple parallel veins in the lamina then a close comparison can be drawn with the smaller (distichous) foliar twigs assigned to *Araucaria* sp. cf. *A. mesozoica* from the Winton Formation of the Eromanga Basin (McLoughlin et al., 1995). Walkom's (1918, pl. 1, fig. 6) ?*Pterophyllum* sp. appears to be a poorly preserved example of *E. baddowensis*.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Maryborough Basin, Queensland.

ORDER UNCERTAIN

Ginkgophyllum Saporta 1875

TYPE SPECIES. *Ginkgophyllum grassertii* Saporta 1875; Permian, Lodève, France.

Ginkgophyllum sp. (Fig. 8E)

Ginkgo digitata (Brongniart) Walkom, 1918: p. 9; pl. 2, figs 4,5.

MATERIAL. GSQF850.

DESCRIPTION. This spatulate leaf is >23mm long (base not preserved), 19.5mm wide; the widest point occurring 9mm from the apex. Proximal to the widest point the leaf's margins are entire and taper acutely towards the base. The apical margin is deeply dissected into five or six narrowly rectangular to slightly spatulate lobes 2.5-4.5mm wide (Fig. 8E). Notches between these lobes are narrowly acute and 2-10mm deep. The apices of the lamina lobes are poorly defined but range from broadly rounded to gently undulate or slightly toothed. The venation is mostly indistinct. It consists of sub-parallel, sparsely dichotomous veins that gently arch in the distal part of the lamina and terminate along the distal margin of the apical lobes. Vein density is around 28 per 10mm across the distal part of the lamina.

REMARKS. Although the base is not preserved, the gently tapering margins of the available specimen suggest that the leaf was not strictly petiolate, a feature more reminiscent of the leaf bases of early Mesozoic seed-ferns such as *Sphenobaeira* and *Kannaskoppifolia* (Anderson & Anderson, 1989; in press) rather than the Ginkgoaceae. Apart from *Ginkgophytopsis truncata* sp. nov. (described below) other fan-shaped leaves with dichotomous venation from the Australian Lower Cretaceous (see Walkom, 1919; Douglas, 1965; Drinnan & Chambers, 1986; McLoughlin et al., 1995) consistently have

petiolate bases and can be more confidently attributed to the Ginkgoaceae. *Ginkgophytopsis truncata* differs from *Ginkgophyllum* sp. by its non-dissected, truncate apex. The former also has sparse cross-connections between the veins although this feature may not be discernable in *Ginkgophyllum* sp. owing to the poor preservation of venation details.

DISTRIBUTION. Known only from the type formation.

***Ginkgophytopsis* (Høeg)
emend. Retallack 1980**

TYPE SPECIES. *Ginkgophytopsis flabellata* (Lindley & Hutton) Høeg 1967; Newcastle Coal Measures (upper Carboniferous), England.

***Ginkgophytopsis truncata* sp. nov.
(Fig. 8D)**

Ginkgo sp. Walkom, 1918: p. 9; pl. 2, fig. 6.

ETYMOLOGY. For the truncate apex of the leaf.

MATERIAL. HOLOTYPE: GSQF964; Maryborough Formation (Aptian or earliest Albian); Baddow Quarry (Corporation Quarry), Maryborough, Queensland, Australia.

DIAGNOSIS. Cuneate leaf with truncate apex, subparallel venation with most dichotomies developed on the marginal vein, rarely amongst veins of the central lamina. Leaf length:width ratio $>2:1$. Vein anastomoses rare.

DESCRIPTION. Leaf is cuneate, >65 mm long (base not preserved; estimated total length = 82 mm), and reaches a maximum width of 29 mm at the apex. The margins are entire and taper gently towards the base. The apex is sharply truncate. Veins are mostly parallel to subparallel. Marginal veins (located 0.5 mm inside the lamina margin) regularly dichotomize to produce inner lamina veins which in most cases run the length of the leaf and terminate at the apical margin without further dichotomies (Fig. 8D). In a few cases these inner lamina veins undergo a further dichotomy or more rarely they recombine with adjacent veins. Vein density ranges from 20 per 10 mm near the leaf base to around 14 per 10 mm at the apex.

REMARKS. This form is one of the largest foliar fragments in the fossil assemblage. It is unclear whether the apex of the illustrated specimen is complete or whether the leaf has been broken transversely below the apex. A sharply truncate apex is consistent with several other *Ginkgo*-like

leaves recorded from the Gondwanan Early Mesozoic (Retallack, 1980; Anderson & Anderson, in press). However, if the apex has been detached then this leaf form may be conspecific with *Ginkgophyllum* sp. with which it shares a number of additional characters. Both leaves are atypical of the Ginkgoaceae sensu stricto in lacking a petiole. The specimen with sparsely reticulate venation is here assigned to the form-genus *Ginkgophytopsis* following the usage of Retallack (1980) without inferring a natural affinity with the Ginkgoaceae. Retallack (1980) recognized six species in this genus. *Ginkgophytopsis truncata* sp. nov. differs from the other species by its truncate apex and predominance of vein dichotomies adjacent to the leaf margins. It is possible that these leaves are late-surviving representatives of fan-leaved seed-fern groups that included *Kannaskoppifolia* and *Sphenobaiera*, which were more abundant and diverse in the early Mesozoic.

DISTRIBUTION. Known only from the type formation.

INCERTAE SEDIS

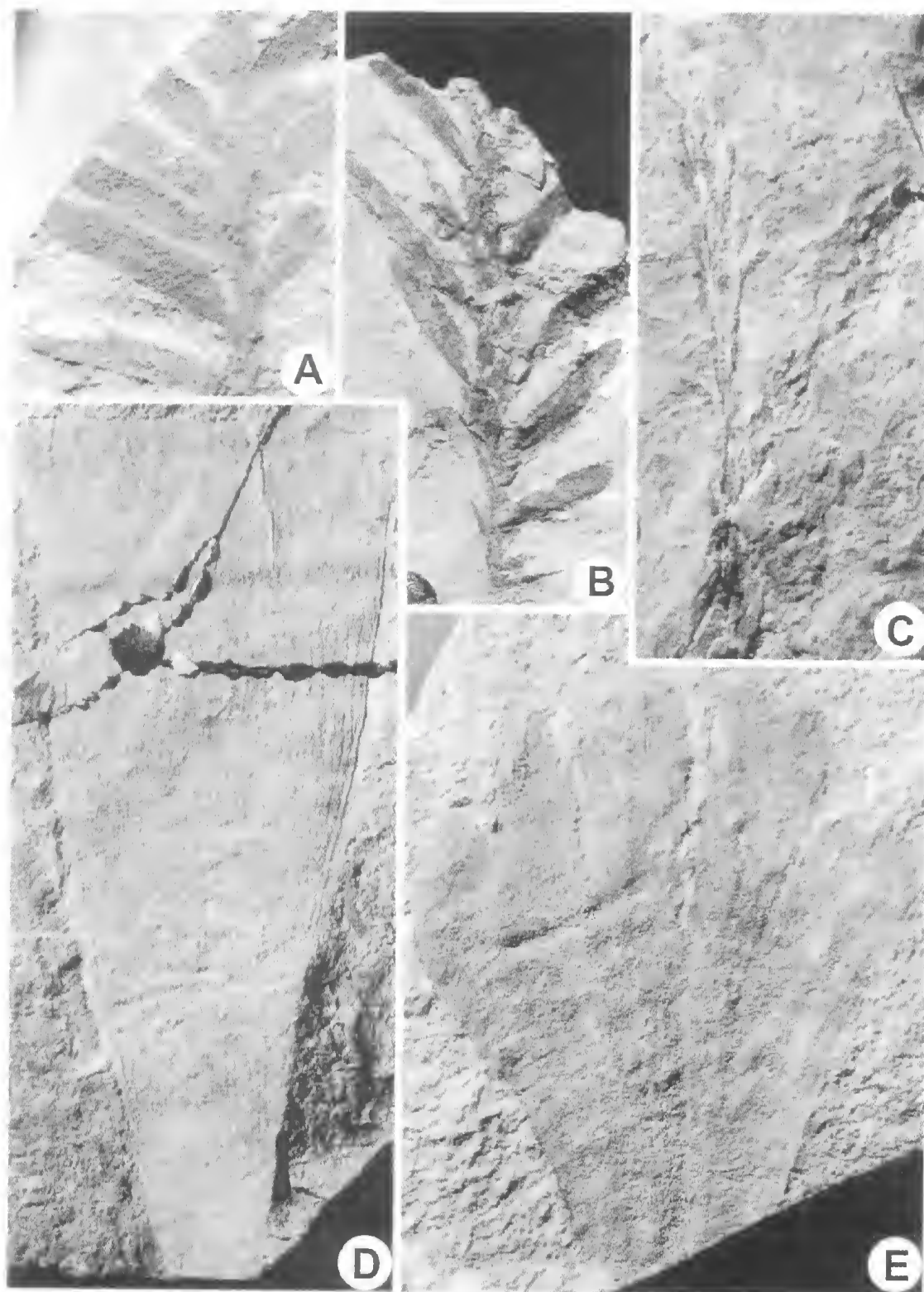
***Equisetalean diaphragms or
gastropod opercula*
(Fig. 9A,B)**

Equisetites sp. cf. *E. rajmahalensis* Oldham & Morris.
Walkom, 1918: p. 5; pl. 1, fig. 8.

MATERIAL. GSQF852, NHMV24604.

DESCRIPTION. Circular organs 15 mm in diameter consisting of an inner disc and an outer ribbed rim. The inner disc is either featureless or has a low, indistinct spiral ridge (Fig. 9B). The rim is marked by a 1.5 mm wide zone of radially arranged ridges and grooves, each around 0.5–1 mm wide (Figs 9A,B).

REMARKS. Walkom (1918) assigned these fossils to *Equisetites* sp. cf. *E. rajmahalensis* Oldham & Morris. Tenton-Woods (1884) illustrated similar equisetalean axis diaphragms from the Walloon Coal Measures (Jurassic) of the Moreton Basin and Walkom (1915) also figured comparable impressions from the Stanwell Coal Measures (Neocomian) near Rockhampton. Although no foliage is preserved with either the Maryborough or Stanwell fossils their similarity to equisetalean remains illustrated elsewhere probably led him to interpret the fossils as nodal diaphragms. The marginal ribs may correspond to either the positions of vascular bundles or indentations in the diaphragm adjacent to radially



disposed leaves. However, equisetalean nodal diaphragms typically have more prominent radiating grooves/ridges corresponding to vascular bundles that extend from a small, central vascular ring to the diaphragm margin (Gould, 1968). Both the Maryborough and Stanwell fossils are associated with marine fossils and could be alternatively interpreted as gastropod opercula with marginal teeth and sockets. The indistinct spiral ridge in the centre of one specimen (GSQF852: Fig. 9B) supports this interpretation but a lack of preserved carbonaceous matter or shell material precludes confirmation of either interpretation.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Maryborough Basin; conspecific or closely related forms occur in the Stanwell Coal Measures (Neocomian), Yarrol Block.

INVERTEBRATE BURROWS

Chondrites (Brongniart) Sternberg 1833

TYPE SPECIES. *Chondrites targionii* (Brongniart) Sternberg 1833; by subsequent designation of Andrews (1955); age uncertain, England.

Chondrites sp. (Fig. 9C)

? Roots. Walkom, 1918: p. 14; pl. 2, fig. 9.

MATERIAL. GSQF841, GSQF846, NHMV24612.

DESCRIPTION. Burrows, circular in cross-section, 1–1.5 mm wide, and reaching in excess of 32 mm long. The burrows are variably orientated with respect to bedding and show sparse branching and cross-cutting relationships (Fig. 9C). The burrows are generally filled with white to grey mud or fine silt, and are typically paler than the siltstone to very fine sandstone host sediments. The burrows lack obvious linings.

REMARKS. Walkom (1918) tentatively regarded these fossils as the remains of plant roots but he also considered the possibility that they represented 'worm-casts'. His preferred interpretation as roots was based on his observation that the fossils had a whorled arrangement of appendages. Re-examination of Walkom's (1918) illustrated specimen, its counterpart in the

Natural History Museum, London, and associated specimens in the Geological Survey of Queensland collections failed to support a whorled interpretation of the fossils. We argue that their irregular branching and sediment-filled structure favours interpretation as invertebrate burrows and this is supported by a marine depositional environment for the host rocks based on the associated rich invertebrate fossil assemblage (Fleming, 1970). The fossils probably represent feeding structures (Fodinichnia) of infaunal invertebrates (Simpson, 1975).

AGE OF THE ASSEMBLAGE

Plant remains preserved in the Maryborough Formation are co-fossilised with an abundant but relatively low-diversity, marine, invertebrate fauna dominated by bivalves. Invertebrate assemblages from the upper part of the formation in the eastern part of the basin (from the same beds hosting the plant remains) have been regarded as indicative of an Aptian age (Etheridge, 1872; Whitehouse, 1926a,b; Day, 1963; Fleming, 1966a,b,c; 1970; 1976; Barnbaum, 1976). Exposures in the Gundiah area in the southwestern part of the basin have yielded assemblages considered to be of Neocomian–?Barremian age (Fleming, 1966a,b,c, 1970, 1976; Day, 1969). However, palynological studies of bore-core samples from the same area have indicated a wholly Aptian age for the Maryborough Formation (McKellar, 1980). Helby & Partridge (1977) assigned a late Neocomian to early Aptian age for palynomorph assemblages from the basal Maryborough Formation in the eastern part of the basin. Cranfield (1993) indicated an early Aptian to ?early Albian age for the unit in the central part of the basin based on preliminary studies of foraminifera and radiolarians. Walkom (1918) assigned a broad, Early Cretaceous age to the plant fossil assemblages from the Maryborough Formation. Most of the plant taxa recognized in the Maryborough Formation (Table 1) have distributions either restricted to the host unit or they are wide-ranging throughout the Early Cretaceous of Australia. However, the presence of *Phyllopteroides serrata*, a stratigraphic index taxon in southeastern Australian basins (Cantrill & Webb, 1987) favours an Aptian or earliest Albian age for the upper part of the formation.

FIG. 8. A, B, *Elatocladus baddowensis* sp. nov.; A, details of leaf insertion on the axis, GSQF838 $\times 4$; B, twig with oblong to lorate leaves, GSQF7267 $\times 2$. C, *Pagiophyllum* sp., branched axis with tightly appressed, awl-shaped leaves, NHMV24614 $\times 4$. D, *Ginkgophytopsis truncata* sp. nov., cuneate leaf with sparsely anastomosing veins, GSQF964 $\times 2$. E, *Ginkgophyllum* sp., apical fragment of leaf showing terminal notches, GSQF850 $\times 4$.

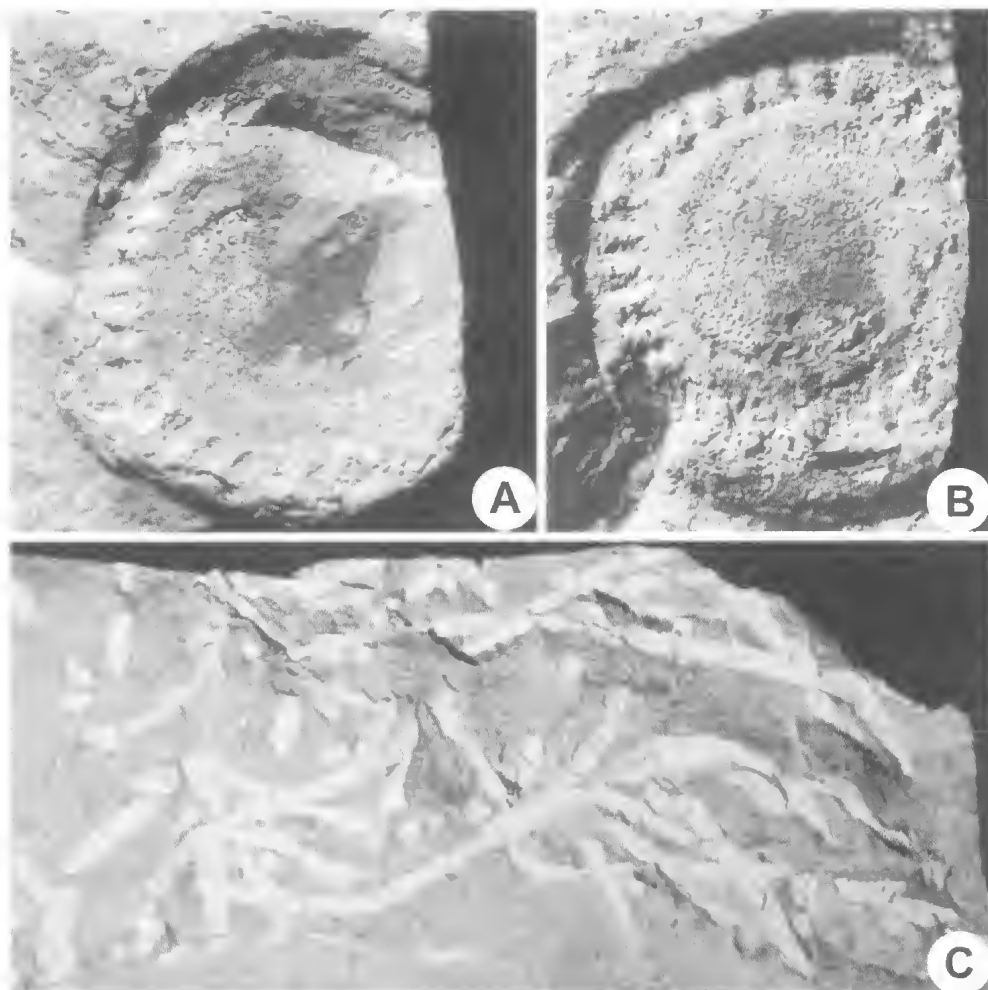


FIG. 9. A, B, circular fossils representing equisetalean nodal diaphragms or molluscan remains with a rim of regular ridges and sockets; A, NHMV24604 $\times 4$; B, GSQF852 $\times 4$ (counterpart of Fig. 9A illustrated in reverse orientation). C, *Chondrites* sp., irregular, mud-filled burrows showing sporadic branching and cross-cutting relationships, NHMV24612 $\times 2.5$.

PALAEOENVIRONMENT

The basal, conglomeratic part of the Maryborough Formation was deposited in fluvial depositional environments (Draper, 1971). The middle part of the formation includes a mixture of black mudstones, green glauconitic sandstones, dark grey shales with invertebrate fossils, and conglomeratic units with scoured bases. These features have been interpreted to reflect deposition within a beach-barrier to shallow marine complex (Cranfield, 1980, 1993). The abundance of invertebrate shells and trace fossils in the upper part of the Maryborough Formation suggests the prevalence of marine conditions.

However, the occurrence of relatively well-preserved plant foliage and fruiting structures suggests that deposition of some beds occurred close to terrestrial environments in relatively low-energy settings. The complex anastomosing burrow-forms within the predominantly fine-grained, lenticular, wavy laminated to symmetrically (wave) rippled sediments are also indicative of quiet-water conditions with only minor reworking by waves. Thin beds containing disarticulated, abraided, and regularly orientated bivalve shells near the top of the formation indicate periodic episodes of higher energy conditions involving wave or current reworking of the sediment (Barnbaum, 1976). Fleming

TABLE 1. Comparison of taxonomic identifications of Maryborough Formation fossil plants by Walkom (1918), and in this study.

Walkom (1918)	This study
<i>Sphenopteris</i> sp.	<i>Phyllopteroides serrata</i> Cantrill & Webb
<i>Taeniopteris elongata</i> sp. nov.	<i>Taeniopteris daintreei</i> McCoy
<i>Taeniopteris tenison-woodsii</i> (Etheridge Jr)	<i>Taeniopteris daintreei</i> McCoy
<i>Taeniopteris</i> sp.	<i>Taeniopteris daintreei</i> McCoy
<i>Ptilophyllum</i> (<i>Williamsonia</i>) <i>pecten</i> (Phillips)	<i>Otozamites</i> sp.
? <i>Pterophyllum</i>	<i>Elatocladus baddowensis</i> sp. nov.
<i>Araucarites polycarpa</i> Tenison-Woods	Araucariacean ovulate cones
<i>Araucarites mesozoica</i> sp. nov.	<i>Podozamites mesozoica</i> (Walkom) comb. nov.
<i>Araucarites</i> sp.	Araucariacean ovulate cones
<i>Pagiophyllum jemmetti</i> sp. nov.	<i>Pagiophyllum jemmetti</i> Walkom
not mentioned	<i>Pagiophyllum</i> sp. A
? <i>Taxites</i>	<i>Elatocladus baddowensis</i> sp. nov.
<i>Ginkgo digitata</i> (Brongniart)	<i>Ginkgophyllum</i> sp.
<i>Ginkgo</i> sp.	<i>Ginkgophytopsis truncata</i> sp. nov.
<i>Equisetites</i> sp. cf. <i>E. rajmahalensis</i> Oldham & Morris	Equisetalean nodal diaphragms or gastropod opercula
?Roots	<i>Chondrites</i> sp. (invertebrate burrows)

(1970) suggested that the invertebrate fauna's low-diversity may be indicative of cold-water conditions in the Early Cretaceous, however, the limited faunal diversity may alternatively reflect environments under the influence of restricted water circulation, low oxygen levels, or high salinity. The collective palaeontological and sedimentological characteristics of the upper Maryborough Formation suggest that it was deposited in a range of shallow marine settings where plant-rich units were deposited in low-energy coastal lagoons or marine embayments.

ACKNOWLEDGEMENTS

Dr Susan Parfrey kindly permitted access to fossils held in the palaeontological collections of the Geological Survey of Queensland. Tiffany Foster and Dr Paul Kenrick are thanked for providing access to the collections of the Natural History Museum, London. S.M. and A.M.D. received support from an Australian Research Council Small Grant. A.-M.T is supported by an Australian Postgraduate Award (Industry) sponsored by the Basin Studies section of the Department of Natural Resources and Environment, Victoria, Cultus Petroleum, SANTOS, and Oil Company of Australia.

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